THE

AMERICAN NATURALIST

VOL. XL | *July, 1906* | NO. 475

ADAPTIVE MODIFICATIONS OF OCCIPITAL CONDYLES IN MAMMALIA

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HISTORICAL

A NUMBER of papers have been written on the occipital condyles but they deal with them from either an ontogenetic or a phylogenetic standpoint. Osborn (:00) has shown that certain of the mammals, such as Tachyglossus (Echidna) and Cercoleptes, possess but a single tripartite condyle continuous across the median plane by a narrow bridge; that others, such as Lutra, have the condyles widely separated and that between these two extremes there are intermediate stages, showing thus that the "mammalian occipital condyles arose from a reptilian tripartite type by the reduction of the median basioccipital element and the expansion of the lateral exoccipital elements."

Gadow (:02), from a study of the anterior cervical vertebræ in the various vertebrates, comes to the conclusion that "the original craniocervical joint must have been a paired one, formed by the lateral occipitals with their more or less serially homologous parts, the neural arches of the first free vertebra. A single condyle could be formed only after the centrum of the first vertebra had been withdrawn as the odontoid process, so as to let the neural arches and the ventral unpaired piece of the atlas . . . . form a cup." Hence he reverses Osborn's order and looks upon the "monocondylar, essentially basioccipital knob, as the final outcome of evolution, independently arrived at by various groups of Sauropsida."

The origin of the condyles needs to be examined further from

this point of view, attention being paid especially to the "proatlas" which Broom (:03) has described in Gomphognathus and Trirachodon. It also occurs in the Rhynchocephalia and the Crocodilia, and Broom predicts that it will yet be found in most of the primitive reptilian types.

Fischer (:01) has shown that in the embryo of the European mole (*Talpa europæa*) the lateral condyles are confluent around the base of the foramen magnum, while in the adult they are separate. He apparently supports Osborn's position in the following sentence: "The most important thing to me is the fact that the configuration of the occipital joint in our mole occupies a sort of intermediate position between the mammals and the Sauropsida."

From a study of the chondrocranium of *Lacerta agilis*, Gaupp (:00) directly supports Osborn. He finds four craniovertebral connections: a dorso-median (the ligamentum apicis dentis), the two lateral corresponding with the lateral condyles of the mammals, and a ventro-median (the median basioccipital element of Osborn) which connects the two lateral parts in the Sauropsida, but which is lost in the mammals. However, he is mistaken in saying (p. 493) that a direct articulation of the ventral part of the atlas with the ventral surface of the basioccipital is lacking in the mammals, for although such an articulation does not occur in the generalized forms, it does occur in some of the specialized, such as Cercoleptes, Gulo, and Taxidea.

General Adaptation of Condyles

The object of the present paper is to point out the types of condyles found among the mammals and to give, so far as possible, the adaptive significance of the several types.

Some 2500 skulls belonging to the American Museum of Natural History and to Columbia University have been examined, and I wish to thank Professor Osborn for his help and suggestions which he has so willingly given.

The occipital condyles are very important, since it is by them that the head articulates with the neck. The head can usually be moved freely in all directions, and in some animals is frequently subjected to great strains, and in order that it may not be dislocated

easily the condyles have become modified in various ways. After giving the various modifications I will attempt to correlate the different types with the habits of the animals, giving, so far as possible, a mechanical explanation for the unusual forms.

They can only be understood in connection with (1) the atlas and axis and (2) the musculature of the occiput and neck. There is a mechanical balance of the ligaments and opposing muscles so that the head is held, with the least amount of effort, in its normal resting position.

The degree of mobility is directly correlated with the curvature of the condyles, and to some extent with their sessile or pedunculate position (Fig. 12, *a* and *d*). The sessile condition never occurs except when the neck is short. When the head can be turned through a large arc the condyles are strongly curved and pedunculate. This is beautifully shown in the birds, in which the single median condyle is pedunculate and hemispherical, an arrangement that permits free motion in all directions. Fig. 12, *e*, shows a sagittal section through a hawk's condyle and *f* a transverse section. The transverse diameter of the two condyles together is always greater in the mammals than the fore-and-aft diameter.

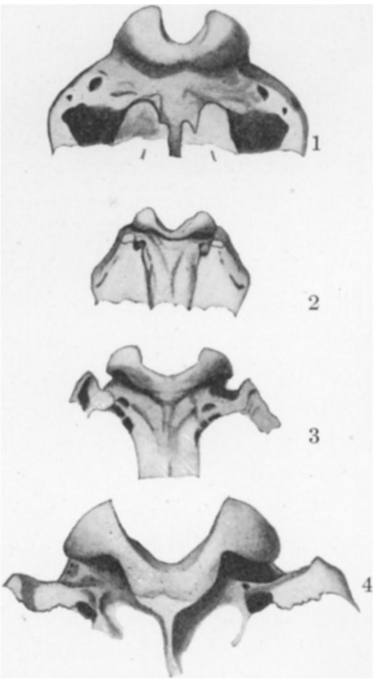
There are three ways of moving the head: up and down, sideways, and in a torsional or twisting manner. Among the mammals, the movement up and down occurs mostly between the atlas and the skull. The torsional movement is mainly between the atlas and the axis, the odontoid process acting as a pivot around which the atlas revolves. To move the head sideways all the cervical vertebræ come into play.

Transition between Monocondylic and Polycondylic Conditions

The monocondylic tripartite and dicondylic conditions are well illustrated in Osborn's paper (:00), the dicondylic condition being derived from the monocondylic by the reduction of the median element.

But reduction does not always occur in the median plane. In some specimens of Gulo the condition is monocondylic (Fig. 4), while in others reduction has taken place, not in the median plane,

but at some distance each side of it, producing a tricondylic condition. This third condyle (Fig. 6, *b*), articulates with the basal part of the atlas when the head is bent downwards sharply, and may be known as the "median condyle." In many mammals the odontoid process is long and when the head is thus sharply bent upon the neck, the process comes in contact with the basioccipital producing a facet (Fig. 6, *a*), which we will call the "odontoid condyle." In the sea otter, *Latax lutris* (Fig. 7), the odontoid and median condyles have each been divided by a depression thus producing *four accessory condyles* or six altogether!



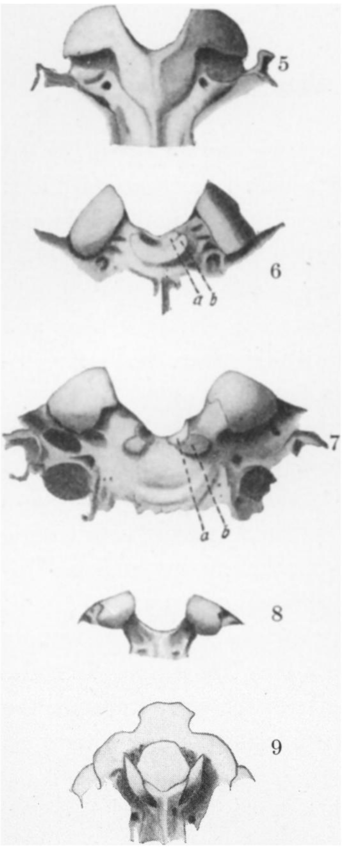
FIGS. 1–4.— 1, Echidna; 2, Putorius; 3, Cercoleptes; 4, Gulo. Types with a continuous tripartite condyle. Gulo shows the condyles prolonged forward, giving a large area of articulation. All $\frac{3}{4}$ natural size.

This is a process of reduction, the articular faces increasing in number but decreasing in total area, possibly to be correlated with the manner of feeding and the character of the food, principally shell fish, the head and neck losing some of their mobility and not being subjected to such great strains as in the more carnivorous forms. It is only comparatively recently that they have adopted their present habits, and so the reduction of the median condylar area has not been carried to the point of obliteration, since the atrophy of an organ always is slower than its development.

Thus we may look upon the condyles of such a form as Erinaceus as representing a generalized type. Here they are separated by an interval equal to one half the diameter of one of them, they are uniformly curved throughout and not prolonged forward, nor are they noticeably sessile or pedunculate.

Adaptation to Carnivorous Habits

As the animal became more carnivorous in its diet, capturing larger animals, the condyles became larger and stronger, extended forward, became approximated, and finally fused, forming a type with a large condylar area (Figs. 4 and 5). Later, as the animal gave up its habit of capturing large prey and took to feeding on smaller animals, the condylar area suffered reduction, since such strong condyles were not needed, the reduction occurring first at each side of the median line (Fig. 6), and later in the sagittal plane (Fig. 7).



Figs. 5–9.— 5, Canis; 6, Taxidea; 7, Latax; 8, Tatusia; 9, Lepus. Types with divided condyles. *a*, odontoid condyle; *b*, median occipital condyle. All ⅞ natural size.

Thus we get a type with the lateral condyles widely separated and poorly adapted for fighting. If, from the generalized type, the animals have adopted habits requiring little or no fighting, and feeding habits requiring no great development of the neck muscles for pulling and tearing, the condyles never acquire a large articulating area, but remain small and tend to become further separated from each other, as in Homo and Tatusia. In both of these, the ancestral forms have the condyles approaching an Erinaceus-like type.

In the early ungulates (Pantolambda, Phenacodus, Hyrachyus, etc.) the condyles are of a generalized type, while in some of the later forms (Ovis, Camelus, Equus) they are highly specialized, being large, and having a peculiar shape. This has probably been brought about by their

manner of fighting among themselves, and will be discussed farther on.

The position of the head upon the neck has a great deal to do with the direction in which the condyles point, whether straight backward, as in the cetaceans, or downward as in man.

Arrangement of Condyles in Different Orders

Monotremata.—The condyles are very thick and rounded (Fig. 1). The odontoid process is long and has a broad basioccipital facet, which, at the sides, may or may not be confluent with the lateral condyles, this being an individual variation.

Marsupialia.— The condyles are, as a rule, pedunculate and strongly convex, and often widely separated. In Didelphys and Dasyurus there is a slight tendency to bridge over the basioccipital, while an odontoid facet occurs in a few.

Insectivora.— In the burrowing forms, Scapanus, Scalops, and Talpa, the neck is very short and the condyles large and sessile, and extended slightly forward, due to the sessile condition and relatively large size. The odontoid process is long, articulating with the basioccipital. In the less specialized forms, such as Erinaceus, the condyles represent a very generalized type.

Cheiroptera.— All the bats have the condyles separated; usually widely so in the Microcheiroptera, where they are sessile. In those forms that carry the head at right angles to the vertebral axis, the condyles point downward, as in man, while in the large Pteropus, they are directed backward.

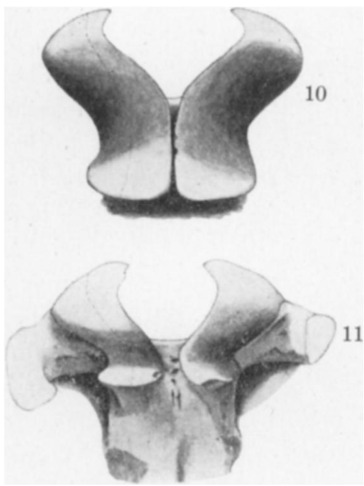
Edentata.— All the living Xenarthra have the condyles very widely separated (Fig. 8), but in Metacheiromys, an armadillo from the middle Eocene, they are nearly in contact ventrally.

Rodentia.— Various conditions are met with among the rodents but none worthy of note except that in Lepus. In this form (Fig. 9), the condyles are not only convex dorso-ventrally, but also transversely, their long axes being directed upward and outward.

Carnivora.— The carnivores very often worry their prey, shaking their heads from side to side, and after it is dead, tearing the flesh from the body. In this latter process the head is sharply flexed upon the neck, so that any further ventral motion is stopped

by the ventral portion of the atlas coming in contact with the median condyle or with the anterior prolongation of the lateral condyles, and, since strong ligaments prevent any dorso-ventral motion between the atlas and the axis, any further strain in this direction will be thrown back upon the other cervical vertebræ, where the processes and muscles are stronger and there is no danger of dislocation. The anterior prolongation of the lateral condyles occurs only in the more strictly carnivorous forms. The median condyle and its separation from the lateral condyles is well shown in the Mustelidæ (Figs. 2–4, 6, and 7). The lateral condyles are usually prolonged forward in the Canidæ and Hyænidæ, and these, together with the Mustelidæ, feed in a standing position, not in a crouching position as do the others.

Cetacea.— All have short necks with a tendency for the cervicals to fuse. The condyles face directly backwards. In all recent forms examined the condyles were sessile and only slightly convex (Fig. 12, *a*). In the Miocene forms (Argyrocetus, Hypocetus, etc.) the condyles were somewhat pedunculate and strongly convex; they had long flexible necks and the head was easily turned, as contrasted with the living cetaceans.

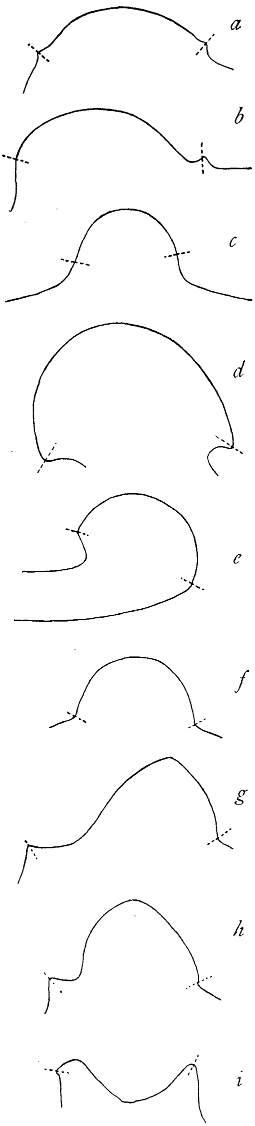


FIGS. 10–11.— 10, Camelus; 11, Ovis. Ungulate types with the condyles prolonged forward. Both ½ natural size.

None of the ungulates has a median condyle, nor an odontoid facet upon the skull, nor are the condyles ever confluent ventrally.

Perissodactyla.— The horses always have the condyles prolonged forward, and they are sometimes slightly concave antero-posteriorly at their forward ends.

Correlated with the downward extension of the condyles is the folding over of the condylar articular surface of the atlas onto its anterior face. The tapirs parallel the horses. Neither the titanotheres nor the rhinoceroses have the condyles prolonged forward.



Artiodactyla.— All the horned ruminants have the condyles extended forward and broadened out and curved downward at their anterior ends. Correlated with this, as in the horses, the articular surface of the atlas is extended downward on its anterior face. In fighting, the head is bent downward so that the points of the horns will project forward towards the foe. In this position the head interlocks with the atlas so that when the two animals come together with a rush, there can be no dislocation.

The atlas and axis are firmly bound together by ligaments, so that the force of the impact is thrown back upon the body and posterior cervicals where there is no danger of a dislocation as there is no sharp flexion. Fig. 12, *h* and *i*, cross sections of the condyle and atlas of the aoudad (*Ovis tragelaphus*), shows how the two are reciprocally curved at their ventral ends. The dotted line of Fig. 11 shows where section *h* was taken. A similar condition occurs in the hornless females and in the camels and horses. The females of the horned forms have probably inherited this peculiarity from the males; no reason is known for its occurrence in the camels and horses.

Primates.— In the lemurs the condyles point backward while in the Anthropoidea

FIG. 12.— *a*, Monodon; *b*, Homo; *c*, Dasyurus; *d*, Rhinoceros; *e*, Archibuteo, sagittal section; *f*, transverse section of same; *g*, Camelus; *h*, *Ovis tragelaphus*; *i*, section through atlas of same. Sections through the left condyle from the median aspect showing the antero-ventral portion to the left and the postero-dorsal to the right. The dotted lines in Figs. 10 and 11 show where sections *g* and *h* were taken. Fig. 12, *i*, a section through the atlas that would be opposite section *h* in its natural position, shows how the condylar articular surface is curved over onto its anterior face. All drawn the same size for comparison.

they are usually placed under the cranium and directed downward. They are always widely separated, except in some of the lemurs. Occasionally the odontoid process articulates with the skull (Homo, Cercocebus, some lemurs); no median condyle occurs. On the median part of the condyles there is usually a depression, which in some forms becomes a sharp notch.

In some of the mammals (Hyæna, Tragulus, Equus, Ovis, Camelus, Figs. 10, 11, and 12, *g*), the articular surface of the condyles, instead of having a continuous curve, possesses a ridge running obliquely outward and upward from about the middle of the inner border of the condyles. No explanation is offered for this peculiar condition as it apparently reduces the efficiency of the condylar articulation. The habitual position of carrying the head, and its direction with reference to that of the atlas, will probably offer some explanation.

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